MOLECULAR ECOLOGY

Molecular Ecology (2012) **21**, 184–194 doi: 10.1111/j.1365-294X.2011.05372.x

Plant dispersal in the sub-Antarctic inferred from anisotropic genetic structure

CÉLINE BORN,* PETER C. LE ROUX,†[1] COLIN SPOHR,* MELODIE A. MCGEOCH†,‡ and BETTINE JANSEN VAN VUUREN*,†[2]

*Evolutionary Genomics Group, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa, †Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa, ‡Cape Research Centre, South African National Parks, PO Box 216, Steenberg 7947, South Africa

Abstract

Climatic conditions and landscape features often strongly affect species' local distribution patterns, dispersal, reproduction and survival and may therefore have considerable impacts on species' fine-scale spatial genetic structure (SGS). In this study, we demonstrate the efficacy of combining fine-scale SGS analyses with isotropic and anisotropic spatial autocorrelation techniques to infer the impact of wind patterns on plant dispersal processes. We genotyped 1304 *Azorella selago* (Apiaceae) specimens, a wind-pollinated and wind-dispersed plant, from four populations distributed across sub-Antarctic Marion Island. SGS was variable with *Sp* values ranging from 0.001 to 0.014, suggesting notable variability in dispersal distance and wind velocities between sites. Nonetheless, the data supported previous hypotheses of a strong NW–SE gradient in wind strength across the island. Anisotropic autocorrelation analyses further suggested that dispersal is strongly directional, but varying between sites depending on the local prevailing winds. Despite the high frequency of gale-force winds on Marion Island, gene dispersal distance estimates (σ) were surprisingly low (<10 m), most probably because of a low pollen dispersal efficiency. An SGS approach in association with isotropic and anisotropic analyses provides a powerful means to assess the relative influence of abiotic factors on dispersal and allow inferences that would not be possible without this combined approach.

Keywords: anisotropic spatial autocorrelations, *Azorella selago*, Marion Island, SGS, wind-dispersal

Received 7 April 2011; revision received 6 October 2011; accepted 17 October 2011

Introduction

Fine-scale spatial genetic structure (SGS; the nonrandom distribution of genotypes) in plants is shaped by various processes, including dispersal, demography and environmental heterogeneity (Loveless & Hamrick 1984; Hamrick *et al.* 1993; Nathan & Muller-Landau 2000; Klein *et al.* 2003; Bohrer *et al.* 2005; Hardy *et al.* 2006). Dispersal represents a complex interaction between an organism and its environment, as dispersal capabilities are strongly influenced by landscape features (e.g. wind exposure, slope angle and topographic heterogeneity) and climatic parameters (e.g. wind speed, wind direction and precipitation)(Bullock & Nathan 2008; Damschen *et al.* 2008; Schurr *et al.* 2008; Wright *et al.* 2008; Kuparinen *et al.* 2009). This may be particularly true for wind-pollinated and wind-dispersed species (Sokal *et al.* 1986; Soons *et al.* 2004; Bohrer *et al.* 2005; Levey *et al.* 2008), especially those growing in windy and/or topographically heterogeneous environments.

Correspondence: Céline Born, Fax: +27 21 808 2405;
E-mail: celineborn@hotmail.com; celineborn@gmail.com
[1]Current address: Department of Geosciences and Geography, University of Helsinki, PO Box 64, FI-00014, Finland
[2]Department of Zoology, University of Johannesburg, PO Box 524, Auckland Park, 2006, South Africa

Spatial genetic structure is typically expressed as the relationship between kinship (relatedness estimates between pairs of individuals) and the physical distance between individuals (Rousset 1997; Hardy & Vekemans 1999, 2002; Smouse & Peakall 1999; Vekemans & Hardy 2004). Most SGS studies have been based on isotropic spatial autocorrelation analyses, which have successfully demonstrated the influence of various factors on species dispersal, including species' life history traits (Vekemans & Hardy 2004; Luna *et al.* 2005; Barbara *et al.* 2008), dispersal vectors (Hardy *et al.* 2006) as well as colonization and recruitment dynamics (Walter & Epperson 2004; Jones & Hubbell 2006; Born *et al.* 2008a,b). SGS has also been used to assess the barrier effect of landscape elements (Frantz *et al.* 2010), and under the assumption of drift-dispersal equilibrium, isotropic SGS analyses can be used to estimate historical gene dispersal (Rousset 1997; Vekemans & Hardy 2004; Hardy *et al.* 2006; Epperson 2007). As a result, isotropic SGS analyses have provided insights into the importance of wind exposure for dispersal, including for example, that gene flow in wind-dispersed or wind-pollinated species is enhanced in fragmented and open areas (Young & Merriam 1994; Nason *et al.* 1997; Born *et al.* 2008a). By contrast, anisotropic spatial autocorrelation techniques, initially proposed to detect anisotropic patterns in large-scale human (e.g. Sokal *et al.* 1986; Falsetti & Sokal 1993) and other mammal genetic structures (Hu *et al.* 2010), have seldom been used to infer directional patterns in fine-scale SGS. A case study for plants was carried out by Dutech *et al.* (2005) using bearing analyses, as proposed by Falsetti & Sokal (1993) and developed further by Rosenberg (2000), to detect anisotropic patterns in the spatial genetic structure in Valley oak (*Quercus lobata*). However, Dutech *et al.* (2005) failed to find evidence for directional dispersal for this wind-pollinated tree species, a result that was later confirmed by Austerlitz *et al.* (2007) using a pollen cloud simulation.

In this study, we combine fine-scale SGS analyses with isotropic and anisotropic spatial autocorrelations to document important differences in dispersal capabilities among populations and to highlight how differences in wind patterns (speed and direction) can influence plant dispersal processes. We demonstrate the efficacy of this approach to infer the relative impacts of wind characteristics on dispersal processes in plants by studying the SGS of a wind-pollinated and wind-dispersed species, *Azorella selago* Hook.f. (Apiaceae), on sub-Antarctic Marion Island. West Wind Drift is thought to be an important vector for propagules across the sub-Antarctic with the majority of the region's flora being wind-dispersed (Huntley 1971). Indeed, the relatively homogenous composition of the sub-Antarctic flora may be due to the consistent and effective dispersal of seeds between islands by these westerly winds (Chown *et al.* 1998; Greve *et al.* 2005; Felicísimo *et al.* 2008). At a finer spatial scale, local wind patterns are expected to control seed and pollen movements and thus to structure species' genetic diversity. We therefore hypothesize that local dispersal in *Azorella selago* would be strongly directional at local spatial scales (owing to the prevailing winds) and that propagules are dispersed over longer distances on the windward side of islands than on their leeward sides. We specifically test these hypotheses on Marion Island, situated approximately 2200 km south-east of Cape Town, South Africa, in a region of strong prevailing westerly winds ('the roaring forties').

To test these hypotheses and demonstrate the differences in dispersal capabilities associated with wind heterogeneity, we genotyped 1304 *Azorella selago* specimens from four populations across Marion Island using seven microsatellite markers. Isotropic SGS analyses (Hardy & Vekemans 2002; Vekemans & Hardy 2004) and gene dispersal estimations were performed and compared among these sites to detect possible differences in dispersal efficacy as a result of differing wind strength. Following this, directional SGS analyses (anisotropic spatial autocorrelations or bearing analyses; Falsetti & Sokal 1993) were conducted to determine the dominant dispersal direction at each site.

Material and methods

Azorella selago *on Marion Island*

The Prince Edward Islands comprise Marion (S 46.5°, E 37.4°) and Prince Edward Island (S 46.6°, E 37.9°) and are situated within the Polar Frontal Zone of the Antarctic Circumpolar Current. The climate is hyperoceanic, characterized by low but stable temperatures (mean temperature, ~6 °C; mean daily temperature range, <3 °C; mean seasonal temperature range ~4 °C), high precipitation (2000–3000 mm p.a.) and humidity (~80%) and near complete cloud cover on most days (Smith 2002; Rouault *et al.* 2005; le Roux 2008). The dominant wind direction is from the westerly sector, as expected from the island's location in a belt of strong large-scale westerly atmospheric circulation. According to the data collected from 1949 to 2008 at the South African Weather Service's meteorological station on the eastern side of the island (Fig. 1), north-westerly winds are strongest (>10 m/s), followed by south-westerly winds (7 m/s; Rouault *et al.* 2005; le Roux 2008). Easterly winds are uncommon and relatively weak. Wind patterns across Marion

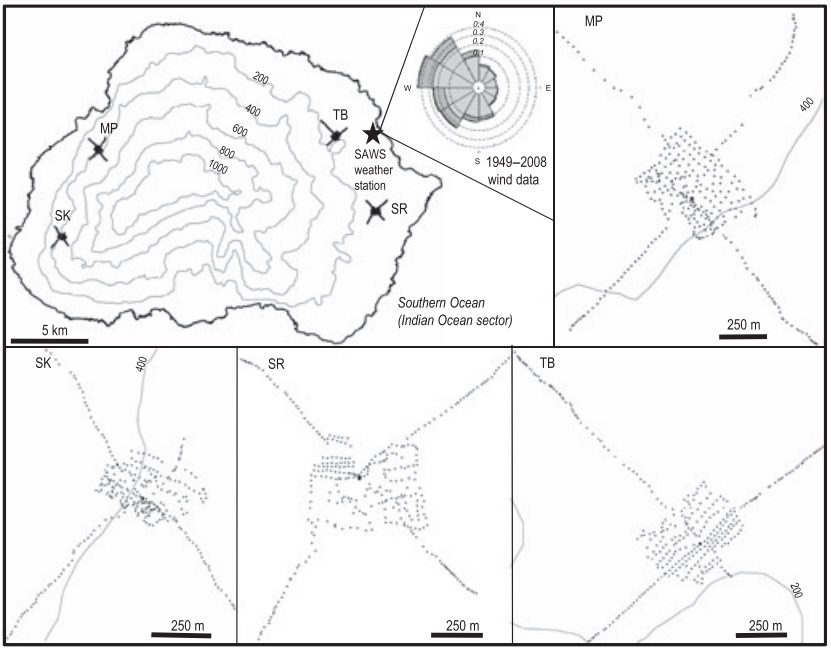

Fig. 1 Sample location on Marion Island. The four sites at which *Azorella selago* was sampled across Marion Island (S 46.5°, E 37.4°; 290 km^2) and the distribution of sampled individuals within each of the four (MP, SR, SK and TB) sites (abbreviations explained in Table 1). The location of the permanent South African Weather Service's meteorological station is indicated with a star, and the wind-rose summarizes wind direction frequency from 1949 to 2008.

Island have changed over the last five decades, with an increasing northerly component (Rouault *et al.* 2005; le Roux 2008). Although it is not unreasonable to suggest heterogeneity in wind patterns across the island (e.g. Chown & Avenant 1992), this has never been verified as long-term data series are not available for other parts of the island.

Azorella selago is a low-growing, compact and streamlined species with a cushion growth form. The species is widely distributed throughout the sub-Antarctica and southern parts of South America and plays an important role as a pioneer species colonizing unstable scoriaceous slopes, recent lava flows and the forelands of retreating glaciers (Huntley 1972; Frenot *et al.* 1993). *Azorella selago* is considered a keystone species on Marion Island, as it hosts diverse epiphyte and invertebrate communities and facilitates the occurrence of many of these species at higher altitudes (Hugo *et al.* 2004; McGeoch *et al.* 2008; le Roux & McGeoch 2010). No pollinators or seed dispersers are known for *A. selago*, suggesting that the species is wind pollinated and wind dispersed and may therefore be particularly sensitive to wind patterns. Pollen release typically occurs during November and December, with seed dispersal occurring from the end of January and lasting for several months (Huntley 1971). During these time periods, north-westerly and westerly winds are predominant on the eastern side of the island (South African Weather Services, unpublished).

Four long-term monitoring sites were selected for this study (see Fig. 1; Table 1): Swartkop Point (SK), Mixed Pickle Cove (MP), Tafelberg (TB) and Stony Ridge (SR). These sites are all located in xeric fell field habitat and are used for monitoring *A. selago* population dynamics (see McGeoch *et al.* 2008 for further details). Cushion densities (*D*) were previously documented and are known to be fairly homogeneous among sites (Table 1).

Wind measurements

Local-scale wind measurements were taken at one of the study sites to validate assumptions made about the relationship between local spatial genetic structure and wind properties. From May 2009, wind speed and direction were logged hourly for 1 year on Junior's Kop, a scoria cone in the vicinity of the TB study site, using Pace WSD-100 sensors combined with either Pace XR5 or Campbell CR200 loggers. Sensors were placed at 220 m a.s.l. on the cone's eastern and western slopes, with each sensor 1 m above the ground surface. These sensors were approximately 200 m from the centre of the TB study site and 1.2 km from the meteorological station.

Table 1 Sampling sites and isotropic SGS parameters

Site	Location	Slope orientation	Latitude	Longitude	Altitude (m a.s.l)	Cushion density (D) (cushions m^{-2})	Sample size	b_{Ld}†,‡	Sp	F_1†,‡	σ_{2D} (m)	$\sigma_{D/10}$ (m)	F_{is}I
SK	Above Swartkop point	E-W	S 46.93°	E 37.57°	288–545	1.2	309	$-0.006^{*/a}$	0.006^{a}	$0.029^{*/a}$	2.1	10.7	-0.02^{NS}
SR	On Stony Ridge	W-E	S 46.91°	E 37.85°	78–159	0.9	334	$-0.013^{*/b}$	0.015^{b}	$0.151^{*/b}$	0.7	5.0	0.17^{*}
TB	Below Tafelberg Plateau	SW-NE	S 46.88°	E 37.82°	100–193	1.1	340	$-0.005^{*/a}$	0.005^{a}	$0.041^{*/a}$	1.7	6.5	0.05^{*}
MP	Above Mixed Pickle Cove	SE-NW	S 46.88°	E 37.65°	249–507	1.1	321	$-0.001^{NS/c}$	0.001^{c}	$0.016^{*/c}$	–	–	0.06^{*}

For each site, kinship coefficient values were regressed on the natural logarithm of the spatial distance between individuals providing the regression slope b_{Ld}. To compare the extent of SGS among populations, Sp statistics were calculated. F_1 is the mean F_{ij} between neighbouring individuals and is approximated by $F(d)$ for the first distance interval (d_{ij} < 12.5 m). Gene dispersal estimates (σ) are bounded by σ_{2D} and $\sigma_{D/10}$ using $2D$ and $D/10$, respectively, as boundary estimates for D_e (D referring to cushion densities). Wright's coefficient of inbreeding (F_{is}) was also calculated for each site.

†To test for SGS, spatial positions of individuals were permuted 9999 times to obtain the frequency distribution of b_{Ld} and F_1 under the null hypothesis that F_{ij} and $\ln(d_{ij})$ were uncorrelated (cf. Mantel test): P values: $^{NS}P \geq 0.05$, $^{*}P < 0.05$.

‡b_{Ld}, Sp and F_1 were compared among sites using t-tests. b_{Ld}, Sp and F_1 significantly differed between sites not sharing letters.

Sampling design

At each of the four sites (SK, MP, TB and SR), leaf samples were taken from 200–220 individuals within a quadrat of approximately 350 × 350 m; in the centre of each quadrat, 20–30 neighbouring plants were sampled, with the remaining 190–200 individuals separated by at least 5 m. An additional 120 individuals were then sampled from four transects (each approximately 750 m in length) that ran from the edge of each sampled quadrat in a NW, NE, SW and SE directions (Fig. 1). This sampling design was adopted to maximize the pairwise spread of distances between individual plants and the angles between pairs of samples for the SGS and anisotropy analyses. The geographic position of each individual was recorded with a handheld GPS unit (eTrex Vista; Garmin). All leaf samples were air-dried and conserved in silica gel.

DNA extraction, genotyping and quality control of the data

Total genomic DNA was extracted using a commercial DNA extraction kit (NucleoSpin® 96 Plant II; Macherey-Nagel). Samples were genotyped using seven species-specific microsatellite markers (Az5, Az6, Az11, Az13, Az14, Az17, Az23; Molecular Ecology Resources Primer Development Consortium *et al.* 2010). Genotyping was performed on an ABI 3730 sequencer (Applied Biosystems), using the GS500LIZ size standard (Applied Biosystems). Results were recovered electronically, and all scoring was carried out using GENEMAPPER 3.7 (Applied Biosystems). The quality of the data was controlled through double scoring the full data set by hand. A total of 1304 specimens were successfully genotyped for at least six of the seven markers, with only 0.3% missing data (see Table 1). No genotyping errors owing to null alleles, large-allele dropout or stuttering were found in our data set using MICRO-CHECKER (Van Oosterhout *et al.* 2004).

Spatial genetic structure and anisotropy analyses

SGS analyses (isotropic spatial autocorrelations; Hardy & Vekemans 2002) estimate the strength of SGS and, therefore, the importance of gene dispersal in shaping the structure of the genetic diversity within each studied site. The strength of the SGS is measured by the slope (b_{Ld}) of the relationship between kinship coefficients (F_{ij}) and the natural logarithm of the spatial distances (d_{ij}) for each pair of individuals (see Fig. 2a), by F_1, the mean kinship coefficient between neighbouring individuals (separated by a maximum of 12.5 m) and by the statistic Sp, derived from b_{Ld} and F_1 [$Sp = -b_{Ld}/(1-F_1)$]. To compare the strength of the spatial genetic structure (and consequently the dispersal dynamics) among sites, we followed Vekemans & Hardy's (2004) procedure based on pairwise kinship coefficients between individuals, using the software SPAGEDI 1.3 (Hardy & Vekemans 2002). Nason's estimator of kinship coefficient (Loiselle *et al.* 1995) was chosen because of its robust statistical properties (Vekemans & Hardy 2004). For each site, kinship coefficient values (F_{ij}) were regressed on the natural logarithm of the spa-

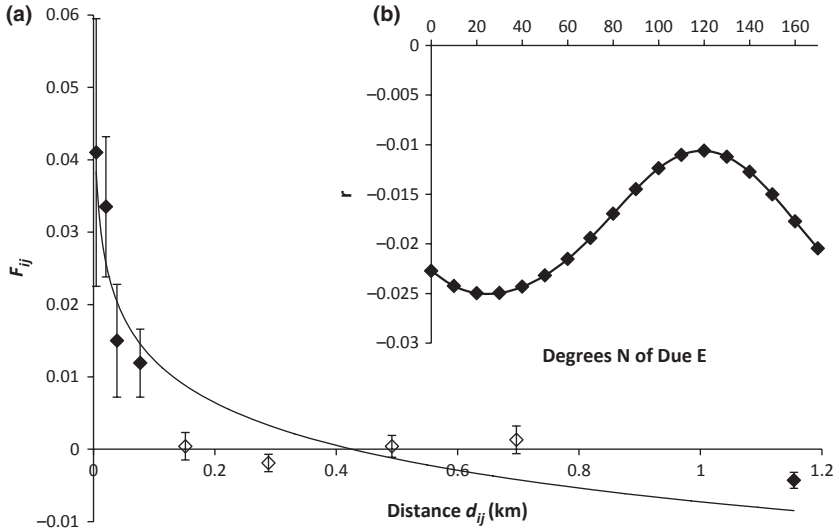

Fig. 2 Spatial genetic structure (SGS) correlogram (a) and anisotropic SGS period diagram (b) for the TB study site. (a) Average kinship coefficient, F_{ij}, plotted as a function of pairwise geographic distances between individuals. Error bars represent standard errors calculated by jackknifing data over each locus. (b) Correlation coefficients, *r*, plotted against bearing. Open symbols indicate the absence of significant differences from the value expected under the null hypothesis of random structure (*P* value >0.05; obtained from 9999 permutations of spatial locations). Spatial genetic structure (SGS) correlogram (a) and anisotropic SGS period diagram (b) for the other sites are given as online Supporting Information (Fig. S1, Supporting Information).

tial distance between individuals, $\ln(d_{ij})$, providing the regression slope b_{Ld} (Rousset 2000). To visualize SGS, kinship coefficient values were averaged over a set of distance intervals (*d*: 0–12.5, 12.5–25, 25–50, 50–100, 100–200, 200–400, 400–600, 600–800 and 800–2000 m), giving *F*(*d*), and plotted against geographical distance. To test the significance of SGS values, b_{Ld} and *F*(*d*), spatial positions of individuals were permuted 9999 times to obtain the frequency distribution of b_{Ld} with the null hypothesis that F_{ij} and $\ln(d_{ij})$ are uncorrelated (cf. Mantel test). Means and standard errors of b_{Ld} and *F*(*d*) were calculated by jackknifing data over each locus. Given that our four sites were sampled using a plot and transect of the same approximate size and were characterized by comparable cushion densities, the differences in the strength of SGS between populations was compared using b_{Ld}, *Sp* and F_1 and using *t*-tests. Wright's coefficients of inbreeding (F_{is}) were also calculated using SPAGEDI 1.3 (Vekemans & Hardy 2004).

At fine spatial scales, SGS should reflect the balance between gene flow and genetic drift [i.e. isolation by distance (IBD) processes]. When comparing subsamples within a site which is characterized by a homogeneous plant density, variation in the strength of the SGS reflects differences in dispersal distances. As pollination and seed dispersal would both be strongly affected by wind direction, we hypothesized the slope of the regression between kinship coefficient values (F_{ij}) and the natural logarithm of the spatial distance between individuals $\ln(d_{ij})$ to be less negative along the wind vector than across it. Along that wind vector, the stronger the wind, the closer b_{Ld} should approximate 0. In other words, we expect negative kinship-distance regression coefficients (*r*) to vary between bearings, with the lowest *r* associated with (i) a bearing orthogonal to the bearing with the highest *r* and (ii) the prevailing wind direction. θ_{MIN} and θ_{MAX}, respectively, refer to bearings associated with the weakest and the strongest negative kinship-distance regressions and are expected be associated with bearings parallel and orthogonal to prevailing wind directions. As prevailing winds are likely to be mainly responsible for gene dispersal in *A. selago*, we also expect b_{Ld} for θ_{MIN} ($b_{Ld\ MIN}$) to be significantly less negative than $b_{Ld\ MAX}$ calculated for θ_{MAX}. Likewise, we also expect F_1 for θ_{MIN} ($F_{1\ MIN}$) to be significantly lower than $F_{1\ MAX}$ calculated for θ_{MAX}. To assess the effects of wind direction on the spatial genetic structure in *A. selago*, we calculated directional autocorrelation following the bearing analysis method (Falsetti & Sokal 1993). Bearing analysis determines the direction of the strongest regression between data distance matrix (**K**) and the geographic distance matrix (**D**). In our study, the **K** matrix is based on kinship coefficient values (F_{ij}) and the **D** matrix on the natural logarithm of spatial distances $\ln(d_{ij})$. **D** is then transformed into 18 new matrices ($\mathbf{D}_0$, $\mathbf{D}_{10}$ to $\mathbf{D}_{170}$), weighting each entry by the squared cosine of the angle α_{ij} [measuring the counterclockwise arc between the positive *x*-axis (east) and the vector connecting i and j and 18 fixed bearings ($\theta = 0°$, 10° to

170°); 0° indicating the *x*-axis (east) and 90° indicating the *y*-axis (north)]. This transformation essentially weights each geographic distance by its alignment with a test direction. Regressions between **K** and $\mathbf{D}_0$, from $\mathbf{D}_{10}$ to $\mathbf{D}_{170}$ are evaluated via Mantel tests with significance determined by permutation tests using PASSAGE 2 (Rosenberg & Anderson 2011). To compare the strength of directional SGS, b_{Ld} and F_1 were then calculated for bearings θ_{MAX} and θ_{MIN}. To maximize the number of individual pairs, a range of 30° around θ_{MAX} and θ_{MIN} was considered. As such, $b_{Ld\ MAX}$ and $F_{1\ MAX}$ were calculated including pairs of individuals with $\alpha_{ij} = \theta_{MAX} \pm 15°$ and $b_{Ld\ MIN}$ and $F_{1\ MIN}$ with $\alpha_{ij} = \theta_{MIN} \pm 15°$. Means and standard errors of b_{Ld} and F_1 were calculated by jackknifing data over each locus. *T*-tests were performed to compare $b_{Ld\ MAX}$, $b_{Ld\ MIN}$, $F_{1\ MAX}$ and $F_{1\ MIN}$ within and among sites.

Estimation of gene dispersal

Wright's neighbourhood size, $N_b \approx 4\pi D_e \sigma^2_g$, where D_e is the effective density of individuals and σ^2 is the mean squared parent–offspring distance, can be estimated as $N_b = -(1-F_1)/b_{Ld}$ when the regression slope b_{Ld} is computed within the distance range $\sigma > d_{ij} > 20\sigma$. As σ is unknown, an iterative approach (implemented in the SPAGEDI 1.3 software; Hardy & Vekemans 2002) can be applied to jointly estimate N_b and σ, if D_e is known. In our case, the cushion densities are known (McGeoch *et al.* 2008 and Table 1; hereafter referred to as *D*). However, as a recent study (Cerfonteyn *et al.* 2011) showed that individual cushions may comprise multiple individual plants, we therefore applied the precautionary principle assuming that population sizes can vary from *D* to 4*D*. D_e can then be approximated as D^*N_e/N. Demographic studies show that N_e/N ratios in adult plant populations typically range from 0.1 to 0.5 (Frankham 1995). We therefore used 2*D* and *D*/10 as boundary estimates for D_e.

Results

At each study site, F_1 is significantly higher than expected under the null hypothesis that F_{ij} and $\ln(d_{ij})$ are uncorrelated (Table 1). This indicates the aggregation of related individuals owing to reduced gene dispersal at very small spatial scales. F_1, b_{Ld} and *Sp* varied between sites, respectively ranging from 0.016 to 0.151, from −0.013 to −0.001 and from 0.001 to 0.015 (Table 1). b_{Ld} are significant for three (SK, TB and SR) of the four sites. For these three sites, isolation by distance (IBD) is likely responsible for the spatial distribution of genetic diversity. For the MP plot, although a significant F_1 was found at small spatial scales, no significant relationship between F_{ij} and $\ln(d_{ij})$ was found. Therefore, reduced gene dispersal may not be the major process involved in shaping genetic diversity in the MP site. F_{is} range from −0.02 (SK) to 0.17 (SR), indicating variation ranging from no inbreeding to high inbreeding rates.

Historical gene dispersal distances (σ) for each site were subsequently estimated, taking 2*D* and *D*/10 as boundary estimates for D_e. These calculations gave σ values ranging from 0.7 m (SR) to 10.7 m (SK; Table 1). Although the range of σ obtained using 2*D* and *D*/10 as boundary estimates for D_e is large, ranging for example from 2.1 to 10.7 m for the SK site, it still provides useful indications of local dispersal distance in *A. selago*.

Bearing analyses based on anisotropic spatial autocorrelation showed significant correlations between pairwise kinship estimates and spatial distance for all 18 fixed bearings (θ = 0°, 10 to 170°; θ in degrees north from due east) for three of the sites (SK, SR and TB; see Figs 2 and S1, Supporting Information). For MP, the relationship between kinship coefficient and the natural logarithm of spatial distance was significant only for a single bearing value, θ = 20°. At all sites, the strength of autocorrelation followed a periodic function against compass direction, with θ_{MIN} and θ_{MAX} (the bearings associated with the weakest and strongest negative correlations) being approximately perpendicular (90–100° difference in bearings; Table 2). Furthermore, the regression slopes $b_{Ld\ MAX}$ were significantly more negative than $b_{Ld\ MIN}$ at all sites, with similar results when comparing $F_{1\ MAX}$ and $F_{1\ MIN}$ (Table 2). These results confirm the importance of anisotropic dispersal in shaping the spatial structure of genetic diversity.

Wind data logged in the vicinity of the TB site (Junior's Kop) show that the mean wind direction on the eastern and western aspects of the landform was similar: East mean = 129° N from due E; West mean = 101°; *n* = 348 days. So, the mean wind direction on both the eastern and western aspects of the landform was approximately from the north-west. These measures of the wind direction are consistent with the long-term wind direction recorded since 1967 at the meteorological station, 1.2 km away (Fig. 1). At the TB site, θ_{MIN} equalled 120° (Table 1; i.e. from NW) and is strongly aligned with the recorded prevailing wind direction for this study site.

Discussion

The dispersal capabilities of organisms play an important role in defining their ability to colonize new areas and to maintain populations in fragmented or dynamic environments. Dispersal capabilities may be variable within species and strongly dependent on environmental conditions, especially for organisms that undergo

Table 2 Estimates of anisotropic SGS parameters

Site	Maximum correlation			Minimum correlation		
	Bearing θ_{MAX} (degrees N from due East)	$b_{Ld\ MAX}$†,‡	$F_{1\ MAX}$†	Bearing θ_{MIN} (degrees N from due East)	$b_{Ld\ MIN}$†,‡,§	$F_{1\ MIN}$‡,¶
SK	150	$-0.010^{*/a}$	0.015^{a}	50	$-0.004^{*/a/*}$	$0.004^{a/*}$
SR	80	$-0.023^{*/b}$	0.150^{b}	170	$-0.002^{*/b/*}$	$0.126^{b/*}$
TB	20	$-0.009^{*/ac}$	0.046^{c}	120	$-0.001^{*/c/*}$	$0.024^{c/*}$
MP	20	$-0.006^{*/c}$	0.047^{d}	110	$0.003^{NS/d/*}$	$-0.023^{d/*}$

For each site, kinship coefficient values were regressed on the natural logarithm of the spatial distance between individuals oriented at a bearing of $\theta_{MAX} \pm 15°$ (i.e. the bearing associated with the strongest spatial autocorrelation) and $\theta_{MIN} \pm 15°$, (the bearing associated with the lowest spatial autocorrelation, Fig. 2), providing the $b_{Ld\ MAX}$ and $b_{Ld\ MIN}$ regression slopes, respectively. $F_{1\ MAX}$ and $F_{1\ MIN}$ were also calculated from these regression results (details in the text).

†To test for SGS, spatial positions of individuals were permuted 9999 times to obtain the frequency distribution of b_{Ld} under the null hypothesis that F_{ij} and $\ln(d_{ij})$ were uncorrelated (cf. Mantel test): P values: $^{NS}P \geq 0.05$, $^{*}P < 0.05$.

‡b_{Ld} and F_N were compared among sites using t-tests. Same letters (respectively a, b, c and d) were used when $b_{Ld\ MAX}$, $b_{Ld\ MIN}$, $F_{N\ MIN}$, or $F_{N\ MAX}$ were not significantly different among plots.

§For each plot, $b_{Ld\ MIN}$ and $b_{Ld\ MAX}$ were compared using t-tests. P values: $^{NS}P \geq 0.05$, $^{*}P < 0.05$.

¶For each plot, $F_{1\ MIN}$ and $F_{1\ MAX}$ were compared using t-tests. P values: $^{NS}P \geq 0.05$, $^{*}P < 0.05$.

passive and wind-assisted dispersal. Across the sub-Antarctic, wind is known to be an important determinant of geomorphological processes (e.g. Hall 2002; Boelhouwers *et al.* 2008) and ecosystem distribution (e.g. Wace 1960; Smith & French 1988) and has been shown to have strong ecological impacts on various organisms (Bate & Smith 1983; Pammenter *et al.* 1986; Hughes 1987; Whinam 1989; Carcaillet 1995; Klok & Chown 1998; Bergstrom *et al.* 2002; Avenant & Smith 2003; Chown *et al.* 2004; le Roux *et al.* 2005). The aim of this study was to empirically highlight spatial variability in the local dispersal capabilities of a sub-Antarctic plant species, which is strongly dependent on wind dynamics.

Contrary to other approaches based on dispersal models (e.g. Soubeyrand *et al.* 2008; Savage *et al.* 2011), spatial autocorrelation methods (SGS and bearings analyses) do not require a priori knowledge of wind characteristics, propagule features or propagule pressure to assess plant dispersal capabilities. SGS strength estimated by Sp values ranged from 0.001 to 0.015 for *A. selago* at the four sites across Marion Island. These values span the whole range of Sp values estimated for other wind-pollinated and/or wind-dispersed species (see Table 2 in Vekemans & Hardy 2004) and highlight the importance of stochasticity and also of context dependence (i.e. local topography) in dispersal processes associated with wind. As all four sites were sampled using the same methodology and were characterized by similar plant densities, differences in the strength of SGS are assumed to reflect variability in gene flow and wind strength between sites. Indeed, a 13-fold variation in b_{Ld} among sites suggests that wind strength is highly variable across the island. These results provide some estimate of the heterogeneity of wind patterns across Marion Island's varied topography and highlight the importance of collecting long-term meteorological data from more than one location in a heterogeneous landscape.

Mean wind speed and the prevalence of westerly and north-westerly winds have been hypothesized to differ between the windward and leeward sectors of the island, with the north-western (windward) sector expected to be characterized by stronger and less variable winds (in addition to higher humidity, greater rainfall and more stable temperatures) than the south-eastern sector (Muñoz *et al.* 2004; Felicísimo *et al.* 2008; le Roux 2008; le Roux & McGeoch 2008). The MP site had the least negative b_{Ld} value (−0.001) and the lowest F_1 value (0.001), which could be attributed to the site being most exposed to strong north-westerly winds. By contrast, the TB and SK sites had intermediate b_{Ld} (−0.005 and −0.006) and F_1 (0.041 and 0.029; Table 1) values, with the SR site having the most negative b_{Ld} (−0.013) and the highest F_1 (0.151). This observed variability in the b_{Ld} slopes and in kinship values calculated for neighbouring individuals (F_1) matches the expected NW–SE gradient in wind strength across the island. Indeed, the lowest SGS (indicating high dispersal efficacy) was observed at the most north-western site (MP) and the strongest SGS at the south-eastern most site (SR), with intermediate SGS slopes observed for the other two sites.

Moreover, as the kinship-distance regression exhibited periodic functions with compass direction for three of our four sites, it is evident that SGS in the study

species is influenced by anisotropic processes, likely due to directional dispersal linked with the species' wind pollination and wind-dispersal syndromes. The bearing associated with the lowest spatial autocorrelation (θ_{MIN}) may therefore indicate prevailing wind direction during pollen release (November and December) and seed dissemination periods (from the end of January to April). At the TB site, θ_{MIN} was 120° (Table 1) and was perfectly aligned with recorded prevailing wind directions (following bearing 101° on the eastern and 129° on the western aspect) recorded 200 m from the site on Junior's Kop. These bearings are also consistent with the wind data recorded at the South African Weather Service meteorological station, 1.2 km from the site. These results strongly support our expectation that θ_{MIN} associated with the lowest SGS indicates the prevailing wind direction during *A. selago* propagule dispersal. Moreover, observed θ_{MIN} was independent of slope orientation, suggesting that seed dispersal by water drainage is not significant compared with wind dispersal.

Values of θ_{MIN} varied greatly between sites (differing by 70° between the SK and TB sites; Table 2). If, as observed for the TB site, θ_{MIN} indicate prevailing wind direction, then, the variation in θ_{MIN} among localities would highlight the influence of local turbulence and/or topography on wind orientation. Subsequently and despite the lack of significance, the MP data set follows an anisotropic pattern with $\theta_{MIN} = 110$ implying that like the TB site, the MP site is probably exposed predominantly to north-westerly winds (Muñoz *et al.* 2004; Felicísimo *et al.* 2008). The directionality at the SR site ($\theta_{MIN} = 170$) has a stronger western component than the other sites, and this result may suggest the influence of Föhn winds, which are relatively common across the eastern sector of Marion Island (le Roux & McGeoch 2008). The wind pattern at the south-western site (SK) may differed most from the other three sites and suggests stronger and/or more frequently south-westerly winds in that area. This result may indicate the presence of local turbulence, likely due to numerous large landscapes features in the immediate proximity of the site (such as Skuinskop peak) disrupting the prevailing north-westerly wind and again highlights the importance of understanding local wind dynamics across the island.

Despite the high frequency of gale-force winds on Marion Island (occurring on >100 days per annum), gene dispersal distance estimates (σ; using $D/10$ as estimates for D_e) are surprisingly low (<10 m; see Table 1). This may reflect local pollen movement being impeded by frequent precipitation (the island on average receives precipitation on 270 days of the year), which may considerably reduce pollen clouds, and by high humidity (mean humidity on the island is >80%) which may accelerate floral dehiscence (Silva Palacios *et al.* 2000; Culley *et al.* 2002). Indeed, the usefulness of wind as a pollen vector *per se* has previously been questioned for another anemophilous sub-Antarctic plant, *Pringlea antiscorbutica*, on Kerguelen Island where autonomous self-pollination is thought to be the best strategy to ensure fertilization (Schermann-Legionnet *et al.* 2007). Self-pollination may explain, for example, the high F_{is} values obtained at the SR site. In addition, our σ inference may only evaluate short distance dispersal (SDD) although long distance dispersal (LDD) process may also play an important role, potentially contributing to a considerable fraction of local pollination for *A. selago* and other sub-Antarctic plant species. Pollen coming from external sources would be homogeneously distributed throughout the study sites and would as such not influence the fine-scale SGS. In our case, σ estimate based on fine-scale SGS would consequently only be informative on SDD and studies considering larger scales would be necessary to complete our understanding of sub-Antarctic plant dispersal. Additional methods are also required to obtain more detailed information on gene flow, particularly separating pollen and seed movement and documenting the shape of dispersal curves after accounting for anisotropy (e.g. Austerlitz *et al.* 2007).

Conclusion

This study empirically highlights the potential of fine-scale isotropic and anisotropic SGS analyses in linking climatic variables with dispersal processes. Specifically, we demonstrate that SGS patterns in *A. selago* show strong heterogeneity across Marion Island. Our results also suggest this variation to be linked to heterogeneity in wind patterns over the island. These results are of particular relevance given that the sub-Antarctic region, including Marion Island, is currently experiencing significant changes in climate. An increase in the influence of the South Indian Ocean anticyclone in the region appears to be responsible for the development of a warmer and drier climate with stronger winds and shifts in the dominant wind direction (Chapuis *et al.* 2004; Rouault *et al.* 2005; Felicísimo *et al.* 2008; le Roux 2008; le Roux & McGeoch 2008). The distribution and survival of sub-Antarctic plant species have already been identified as being sensitive to these changes in climate (le Roux *et al.* 2005; le Roux & McGeoch 2008), and this study now provides evidence to suggest that the region's flora may also experience changes in gene flow and propagule dispersal if the climate continues to change.

Acknowledgements

This research was funded by Stellenbosch University and the South African National Research Foundation (through a South African National Antarctic Programme research grant to BJVV and MAM). CB is the beneficiary of a postdoctoral grant from the AXA Research Fund. Sampling was conducted during the 2009 Marion Island relief voyage, which was logistically supported and funded by the South African Department of Environmental Affairs and Tourism: Antarctica and Islands through the South African National Antarctic Programme. PCLR received additional funding from the Centre for Invasion Biology. We are especially grateful to Mashudu Mashau, Jesse Kalwij and Steven Chown for their generous help in the field, as well as Mia Cerfonteyn and Gayle Pedersen for laboratory assistance. We also thank anonymous reviewers for their helpful and very constructive comments on earlier versions of the manuscript.

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C.B. is interested in plant dispersal ability. For her post-doc study, she is using population genetics tools to characterize plant dispersal at different geographic scales in the sub-Antarctic region. P.C.L.R. is interested in the determinants of species ranges and the influence of biotic interactions on the ecological consequences of climate change. C.S. is a field ecologist. M.A.M. research interests lie in spatial ecology and the consequences of global change for protected areas. B.J.V.V. is interested in the spatial distribution of genetic diversity at different spatial scales, and the processes that drive these.

Data accessibility

Sample locations and microsatellite data have been archived in Dyad with the reference doi:10.5061/dryad.4f1r5vg8.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Spatial genetic structure (SGS) correlogram (a) and anisotropic SGS period diagram (b) for the SR, MP and SK study sites.

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